Redescription and phylogenetic position of the fossil killifish †*Carrionellus diumortuus* White from the Lower Miocene of Ecuador (Teleostei: Cyprinodontiformes)

by

Wilson J.E.M. COSTA (1)

ABSTRACT. - †*Carrionellus diumortuus* from the Lower Miocene of Loja, southern Ecuador, is the type species of †*Carrionellus*, the only American cyprinodontiform genus uniquely containing fossil species. It was first considered as a member of the cyprinodontid tribe Cyprinodontini, a group comprising extant taxa geographically restricted to North and Middle America, but recently it has been tentatively placed in the Neotropical family Anablepidae. †*Carrionellus diumortuus* is herein redescribed on the basis of examination of the type series. Re-evaluation of phylogenetic characters indicates that it is a member of the cyprinodontid tribe Orestiini, which comprises a clade endemic to the Andean region, which may be diagnosed be a unique angled anteroventral profile of the head in the area on the articulation between the lower jaw and the quadrate. †*Carrionellus* is distinguished from *Orestias*, the only other genus of the Orestiini, known only from recent species, by the former genus having tricuspidate jaw teeth, well developed pelvic fin, and 28-29 vertebrae.

RÉSUMÉ. - Redescription et position phylogénétique de †*Carrionellus diumortuus* White, fossile du Miocène inférieur de l'Équateur (Teleostei, Cyprinodontiformes).

†*Carrionellus diumortuus* du Miocène inférieur de Loja, au sud de l'Équateur, est l'espèce type du genre fossile †*Carrionellus*, le seul genre américain éteint de cyprinodontiformes. Ce genre a d'abord été considéré comme un cyprinodontidé membre de la tribu des Cyprinodontini, groupe de genres actuels distribués en Amérique du Nord et Centrale. Plus récemment, il a été rapproché de la famille néotropicale des Anablepidae. L'espèce †*Carrionellus diumortuus* est ici redécrite à partir du ré-examen de la série type. L'évaluation de l'état des caractères phylogénétiques permet de la placer dans une tribu de la famille des Cyprinodontidae, les Orestiini. Cette tribu comprend un clade endémique de la région andine qui peut être reconnu par le profil antéro-ventral de la tête au niveau de l'articulation de la mâchoire inférieure et du carré. Le genre †*Carrionellus* se distingue de l'autre genre de la famille, le genre actuel *Orestias*, par la présence de dents tri-cuspides aux mâchoires, par un plus grand développement de la nageoire pelvienne et par un nombre de 28 ou 29 vertèbres.

Key words. - Cyprinodontidae - †*Carrionellus diumortuus* - South America - Andes - Osteology - Paleontology.

The cyprinodontiform record of South America is scarce, often restricted to tentative preliminary identifications (e.g., Arratia and Cione, 1996; Lundberg, 1998). An exception is †*Carrionellus diumortuus*, described from the Lower Miocene of Loja, Ecuador, by White (1927). It is the type and the only species of †*Carrionellus*, which is the only cyprinodontiform fossil genus of Americas. Although †*C. diumortuus* is known from impression fossils, in which only a few osteological characters are evident, its placement in a strict fossil genus of uncertain phylogenetic position and the presence of several specimens of the type series preserved in different positions make this species the most important cyprinodontiform fossil record for the Neotropical region.

White (1927) first established †*Carrionellus* as a member of the family Cyprinodontidae, which at that time comprised three subfamilies: Cyprinodontinae, Fundulinae and Orestinae (Regan, 1911; Hubbs, 1924). Inclusion of †*Carrionellus* among the Cyprinodontinae by White (1927) was justified by the presence of tricuspid teeth in the jaws (*vs* conical teeth in the remaining subfamilies), which was the only unique diagnostic feature for that group (Regan, 1911; Hubbs, 1924).

The taxonomic position of †*Carrionellus* as a cyprinodontine genus was not challenged until 1981. In a phylogenetic analysis of extant cyprinodontiforms, Parenti (1981) noted that the condition of double row of tricuspid jaw teeth reported by White (1927) differs from the single row of tricuspid teeth occurring in cyprinodontines, suggesting †*Carrionellus* to be a characiform. However, Ghedotti (1998) demonstrated that placement of †*Carrionellus* among cyprinodontiforms is supported by the morphology of the caudal fin, arguing that the presence of multiserial tricuspid teeth is in fact diagnostic for the Neotropical cyprinodontiform family Anablepidae, thus tentatively placing †*Carrionellus diumortuus* in this family.

On the basis of recent examination of the type series, a redescription of †*Carrionellus diumortuus* is provided, including some variability of meristic values and morpho-

(1) Laboratório de Sistemática e Evolução de Peixes Teleósteos, Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Caixa Postal 68049, CEP 21944-970, Rio de Janeiro, Brazil. [wcosta@acd.ufrj.br]

metric data not reported previously. In addition, a revision of informative characters is used to evaluate the phylogenetic position of †*Carrionellus diumortuus* among cyprinodontiforms.

MATERIAL AND METHODS

All material of †*Carrionellus diumortuus* is deposited in the Department of Palaeontology of the Natural History Museum, London (BMNH P). The complete list of comparative material taxa of the families Anablepidae and Cyprinodontidae is given in the Appendix 1, where familial and intrafamilial classification follow Parenti (1981), except for the inclusion of a separate tribe Aphanini, thus better reflecting phylogenetic evidence provided by Costa (1997); additional material of other cyprinodontiform families is listed in Costa (1998). Measurements and counts follow Miller (1948). Osteological preparations of extant taxa were made according to Taylor and Van Dyke (1985).

†*Carrionellus* White, 1927

†*Carrionellus* White, 1927: 519 (type species †*Carrionellus diumortuus* White, 1927 by original designation).

Diagnosis

Distinguished from all other genera of the order Cyprinodontiformes by the unique combination of character states: jaw teeth tricuspidate (*vs* conical, spatulate or bicuspidate), jaw teeth arranged in two rows (*vs* multiple rows or single row), pelvic fin present (*vs* pelvic fin and pelvic-fin support absent).

†*Carrionellus diumortuus* White, 1927
(Figs 1, 2)

†*Carrionellus diumortuus* White, 1927 (original description, Lower Miocene of Loja, Ecuador; holotype: BMNH P. 14320, entire articulated impression specimen, 24.6 mm SL, and BMNH P. 14321, counterpart without caudal fin and posterior portion of caudal peduncle).

Diagnosis

As for the genus.

Description

Morphometric data of holotype and best preserved paratype appear in table I. Dorsal profile slightly convex from snout to end of dorsal-fin base, nearly straight on caudal peduncle. Ventral profile convex from lower jaw to end of anal-fin base, approximately straight on caudal peduncle. Body moderately deep, greatest body deep about 3.5 times in standard length, in vertical just anterior to pelvic-fin base. Head long, about 3.0-3.3 times in standard length. Eye large, occupying about one third of head side. Anteroventral profile of head strongly angled, articulation zone between lower jaw and the quadrate projected, mouth cleft at angle of about 45° to horizontal. Teeth long, weakly tricuspidate, arranged in two rows.

Dorsal fin triangular, anterior rays longer than posterior rays, longest fin length greater than base-fin length; anal fin nearly rectangular, longer than dorsal fin, longest anal-fin length greater than anal-fin base length; caudal fin truncate, longer than anal fin. Dorsal-fin origin posterior to midlength between snout tip and posterior extremity of caudal fin, in vertical approximately through anal-fin origin or slightly anterior to it; first proximal radial of dorsal fin between neural spines of 14th and 15th vertebrae; first proximal radial of anal fin between neural spines of 13th and 14th vertebrae. Pectoral fin long, approximately reaching vertical through pelvic-fin base; pectoral-fin base midway between vertebral column and ventral profile of trunk. Pelvic fin long, slightly longer than anal-fin base; pelvic-fin base approximately midway between pectoral-fin base and anal-fin origin. No contact organs on fin rays. No filamentous rays on fins. Dorsal-fin rays 9-10; anal-fin rays 13-15; caudal-fin rays 30-31; pectoral-fin rays 14-15; pelvic-fin rays 6. Total vertebrae

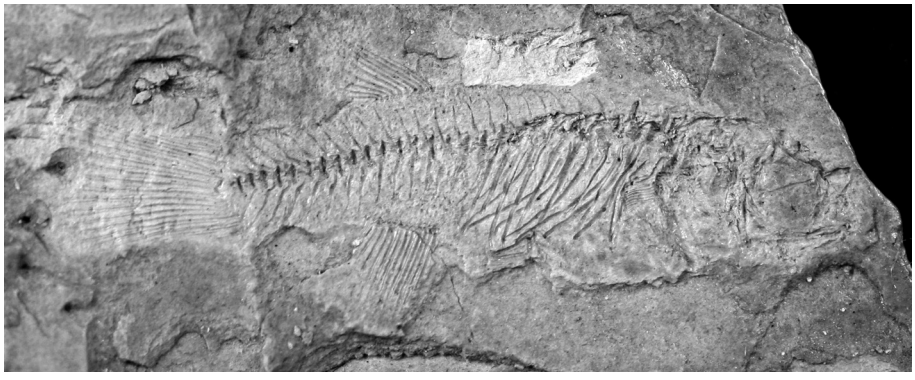

Figure 1. - †*Carrionellus diumortuus*, BMNH P.14320. Holotype in right lateral view, 24.6 mm SL. Lower Miocene of Loja, Ecuador.

28-29 (12 abdominal, 16-17 caudal); last four vertebrae participating of caudal skeleton. Scales cycloid, slightly deeper than wide, without contact organs; about eight radii in scales just below dorsal fin or just above anal fin.

Material examined

Holotype (BMNH P. 14320) and counterpart (BMNH P. 14321), and 27 paratypes, three in counterpart (BMNH P. 14322-50); all collected by Clodoveo Carrión Mora, in Loja, southern Ecuador.

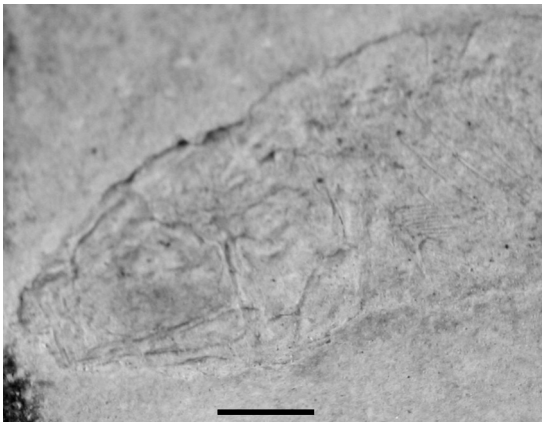

Figure 2. - Head of †*Carrionellus diumortuus* in left lateral view, BMNH P.14339, paratype. Scale bar = 2 mm.

DISCUSSION

In the most recent taxonomic study including †*Carrionellus diumortuus*, this species was tentatively placed in the family Anablepidae by the possession of multiserial tricuspid teeth in the jaws (Ghedotti, 1998), which is considered as a synapomorphy for that family (Parenti, 1981; Ghedotti,

Table I. - Morphometric data of †*Carrionellus diumortuus*.

	Holotype BMNH P.14320	Paratype BMNH P.14331
Standard length (mm)	24.6	26.3
Percent of standard length		
Body depth	28.3	24.9
Caudal peduncle depth	16.0	13.8
Predorsal length	68.4	65.8
Prepelvic length	51.3	49.3
Length of dorsal-fin base	9.5	9.9
Length of anal-fin base	12.2	12.0
Caudal-fin length	26.1	–
Pectoral-fin length	–	17.8
Pelvic-fin length	–	12.7
Head length	30.2	32.3
Percent of head length		
Head depth	81.6	68.8
Eye diameter	34.5	–

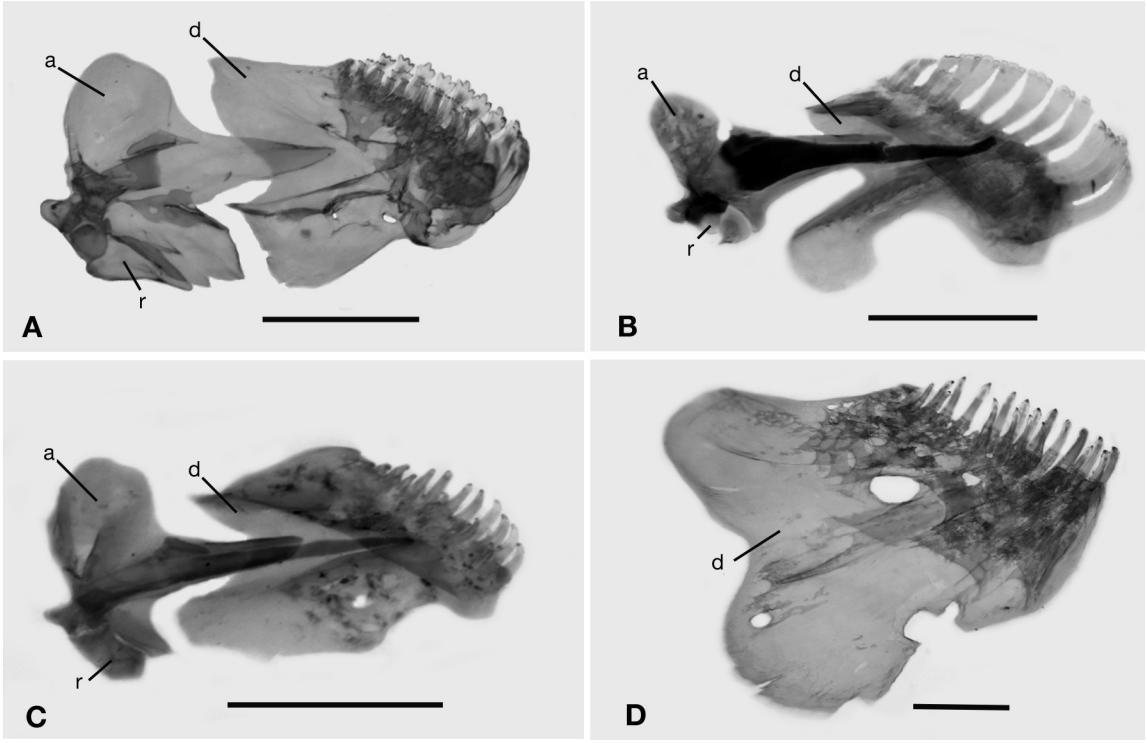

Figure 3. - Left lower jaw, medial view. **A**: *Jenynsia multidentata*; **B**: *Orestias agassizii*; **C**: *Cualac tesselatus*; **D**: *Cubanichthys cubensis*. a: angulo-articular; d: dentary; r: retro-articular. Scale bars = 1 mm.

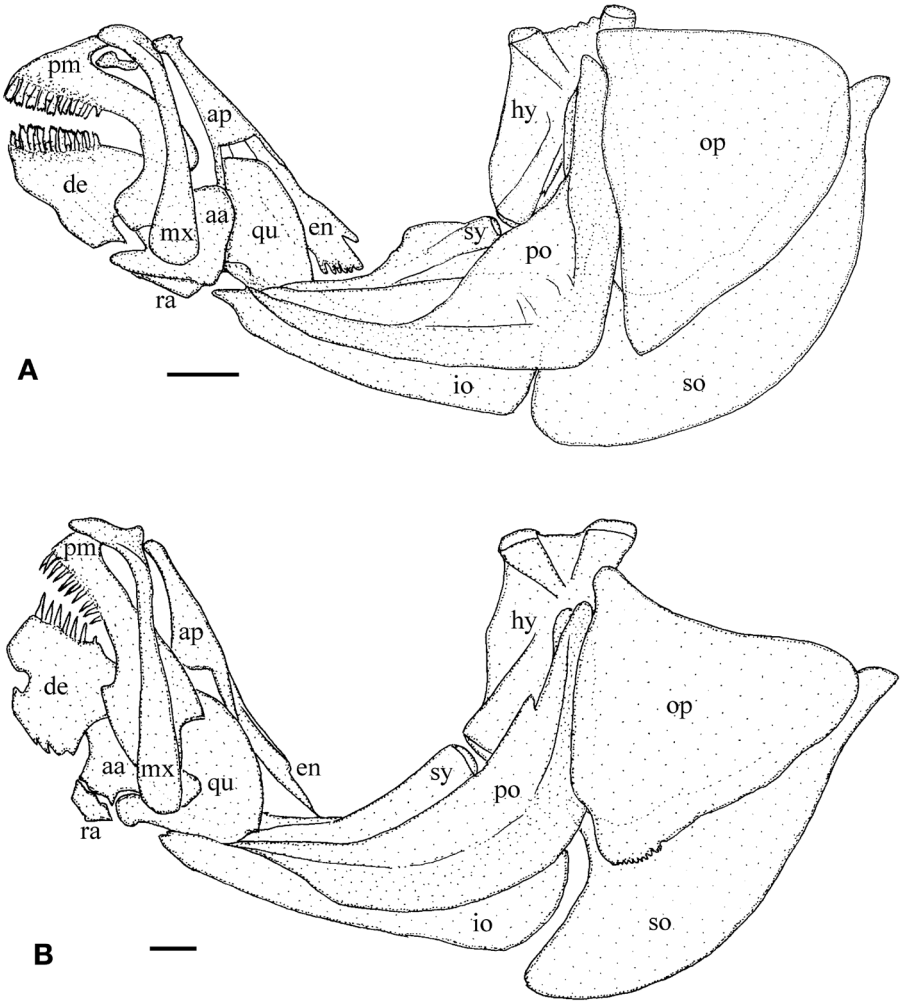

Figure 4. - Jaws, jaw suspensorium and opercular apparatus, left side, lateral view. **A**: *Jenynsia multidentata*; **B**: *Orestias gilsoni*. aa: angulo-articular; ap: autopalatine; de: dentary; en: entopterygoid; hy: hyomandibula; io: interopercle; mx: maxilla; op: opercle; pm: premaxilla; po: preopercle; qu: quadrate; ra: retro-articular; so: subopercle; sy: sympletic. Cartilages are not represented. Scale bars = 1 mm.

1998). However, this diagnostic feature in fact involves the combination of two distinct characters: morphology of teeth and number of tooth rows (Costa, 1997, 1998), which are separately discussed below.

Jaws, teeth, distal region, morphology: (0) conical; (1) tricuspidate (Costa, 1997: ch. 27). As in other atherinomorphs, cyprinodontiforms typically have all the jaw teeth conical, but two cyprinodontiform families, the Anablepidae and Cyprinodontidae, are exceptions (Parenti, 1981; Costa, 1997, 1998; Ghedotti, 1998). In anablepids, tricuspidate jaw teeth are present in species of the genera *Oxyzygonectes* Fowler and *Jenynsia* Günther (Fig. 3A), but are secondarily loss in *Anableps* Scopoli (Ghedotti, 1998, 2000). Among the three most speciose clades of cyprinodontids, the South American orestiines, the North American cyprinodontines and the Old World aphanines, the teeth are always conical in the former (Fig. 3B), and always tricuspidate in the two latter (Fig. 3C). The fourth cyprinodontid clade, the Cubanichthyinae, considered the most basal group of the family, comprises a single genus, *Cubanichthys* Hubbs, with two species: *C. cubensis* (Eigenmann, 1903), a miniature species endemic to Cuba, and *C. pengelleyi* (Fowler, 1939) endemic to Jamaica. On the basis of the examination of *C. cubensis* alone (Fig. 3D), it was generalized that all cubanichthyines have conical teeth, which then would be the basal condition for cyprinodontids (Costa, 1997). However, Ghedotti (2000) found tricuspidate teeth in the jaws of *C. pengelleyi*, making ambiguous the origin of tricuspidate teeth in cyprinodontids, with two possible equally parsimonious hypotheses: either origin in the cyprinodontid ancestor, with subsequent loss in *C. cubensis* and orestiines, or independently origins in *C. pengelleyi* and in the clade comprising cyprinodontines and aphanines. Anyway, the presence of tricuspidate teeth in †*Carrionellus diumortuus* is not enough to permit its unambiguous placement either in the Anablepidae or in the Cyprinodontidae, but makes improbable its inclusion in the remaining eight cyprinodontiform families (Aplocheilidae, Fundulidae, Goodeidae, Poeciliidae, Profundulidae, Not-

hobranchiidae, Rivulidae, Valenciidae), in which teeth are never tricuspidate (Parenti, 1981; Costa, 1998).

Jaws, teeth, rows, number: (0) multiple; (1) single; (2) two (modified from Costa, 1997: ch. 28). Costa (1997) just recognized two states: jaws with an external row of larger teeth and several rows of smaller teeth irregularly arranged, a primitive condition among cyprinodontiforms, and jaw dentition represented by a single row, a derived condition occurring in most cyprinodontids. All anablepids have the plesiomorphic condition for cyprinodontiforms (Fig. 3A). Among cyprinodontids, all cyprinodontines and aphanines have a single tooth row when adults (Fig. 3C), but juveniles may have an additional inner row (e.g., Franz and Villwock, 1972). In cubanichthyines, there is an external row of larger teeth, followed by an inner irregular row of smaller teeth in all ontogenetic stages (Fig. 3D). In *Orestias* Valenciennes, the single genus of the Orestiini, the dentition is variable among different species. In the most basal lineage, the *Orestias agassizii* species group, species have a conspicuous double row (Fig. 3B) whereas in other orestiine taxa teeth are reduced in number and placed in a single irregular series, except in *O. ispi* Lauzanne, in which teeth are absent or sometimes rudimentary (e.g., Parenti, 1984a). The presence of a double tooth row in the early stages of aphanines and cyprinodontines, in the most basal orestiines, and in cubanichthyines, support this derived condition as basal among cyprinodontids. Therefore, the double tooth row dentition of †*C. diumortuus* supports its placement among cyprinodontids.

The placement of †*C. diumortuus* among cyprinodontids was rejected by Ghedotti (1998) due to the putative presence of parietal in that species (*vs* absence in most cyprinodontids). However, examination of all specimens of the type series indicates that the structure suggested as being a parietal by White (1927) and later confirmed by Ghedotti (1998: fig. 26A) does neither have the position nor the shape of a typical cyprinodontiform parietal, probably constituting an artefact of preservation.

More informative than the characters discussed above is a conspicuous morphology of the lower jaw region consistently exhibited in different specimens of the type series of †*C. diumortuus*. It consists of a peculiar angled anteroventral profile of the head in the area comprising the articulation between the lower jaw and the quadrate, as a consequence of the lower jaw being placed almost perpendicular to the main axis of the body (Fig. 2). This strongly contrasts with the slightly curved anteroventral profile of the head of anablepids (Fig. 4A) and most other cyprinodontiforms. Although some cyprinodontids may have the anteroventral profile of the head slightly angled (Parenti, 1981; Costa, 1997), the condition present in †*C. diumortuus* is only comparable to that occurring in species of *Orestias* (Fig. 4B), which is unique among cyprinodontiforms.

The overall compatibility between the morphological features of †*C. diumortuus* and recent cyprinodontids, as well as and the presence of a derived feature of the lower jaw uniquely shared by †*C. diumortuus* and species of *Orestias* support the inclusion of the genus †*Carrionellus* in the Cyprinodontidae, closer related to the extant genus *Orestias* (i.e., as a member of the tribe Orestiine). †*Carrionellus* is easily distinguished from *Orestias* by the presence of tricuspidate jaw teeth, pelvic fin, and 28-29 vertebrae in the former genus (*vs*. teeth conical, pelvic fin and pelvic girdle absent, and 30-38 vertebrae in *Orestias*).

The hypothesized closer relationships between †*Carrionellus* and *Orestias* is not surprising when analysing the geographic distribution of both genera (Fig. 5). †*Carrionellus* is uniquely found in Loja, today placed in the glacial Cuxibamba valley, southern Andean region of Ecuador, with altitudes above 2100 m. *Orestias* is also an Andean genus,

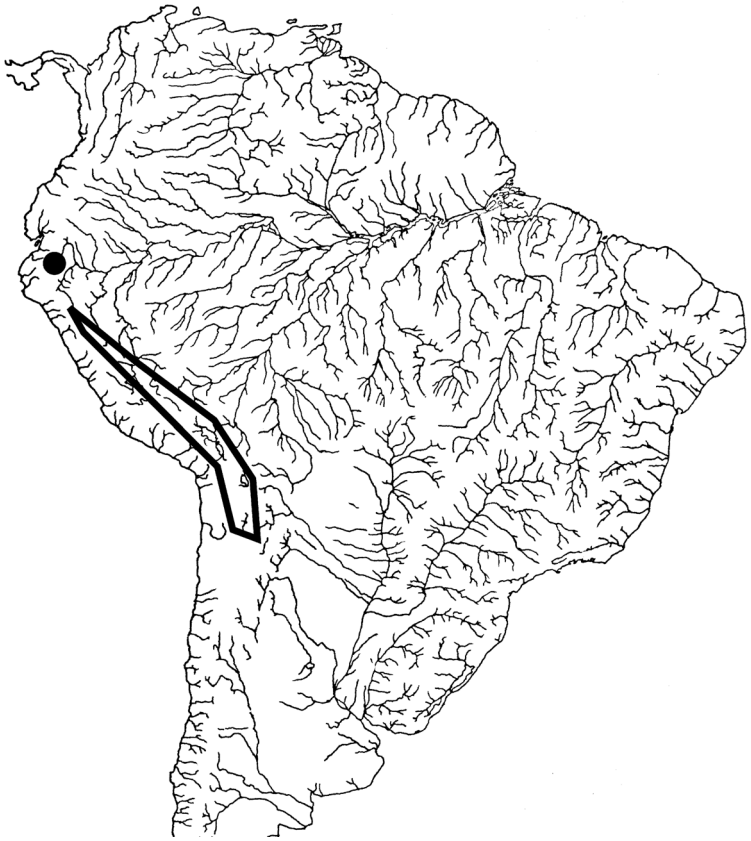

Figure 5. - Geographic distribution of Andean cyprinodontids; dot indicates the single known locality for †*Carrionellus diumortuus*, and the track polygon, the distribution area occupied by the genus *Orestias*.

occurring in lakes and associated streams at high altitudes, between northern Peru and northern Chile (Parenti, 1984a, 1984b).

Lundberg *et al*. (1998) suggested that the extant aquatic biota of the Altiplano basin of Peru and Bolivia, and the fossil aquatic biota of the Ecuadorian Interandean Valley had a common origin in the western Amazon just before the uplift of the Andes between late Paleogene to early Neogene. Recent explorations of isolate Andean lakes of Chile have revealed some endemic, previously unknown species of *Orestias* (Vila and Pinto, 1986; Vila, 2006). Many other isolate lakes of the Andes of Peru and Ecuador are of difficult access and still not exhaustively sampled for fish collections, so the possibility in finding a new recent orestiine taxon closely related to †*C. diumortuus* in the future cannot be excluded.

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Appendix 1. - Material examined

Material is listed alphabetically by family and genus. Catalog number is followed by number of specimens examined, all of which were cleared and stained for bone and cartilage. Institutional Abbreviations are: CAS, California Academy of Sciences, San Francisco (SU means material previously deposited in Stanford University); UFRJ, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro; USNM, National Museum of Natural History, Smithsonian Institution, Washington.

Family Anablepidae: *Anableps dowi* Gill, 1861: UFRJ 3290, 2; Guatemala: Los Cerritos, Río Los Esclavos. *Anableps microlepis* Müller & Troschel, 1844: UFRJ 3420, 2; Brazil: Pará. *Jenynsia multidentata* (Jenyns, 1842): UFRJ 5066, 5; Brazil: Rio de Janeiro, Lagoa Rodrigo de Freitas. *Jenynsia unitaenia* Ghedotti & Weitzman, 1995: UFRJ 3422, 2; Brazil: Santa Catarina, Rio São Bento.

Family Cyprinodontidae: Subfamily Cubanichthyinae: *Cubanichthys cubensis* (Eigenmann, 1903): USNM 331917, 2; Cuba. Subfamily Cyprinodontinae:

Tribe Aphaniini: *Aphanius dispar* (Rüppell, 1829): UFRJ 3302, 2; Kuwait: Al-Khiran. *Aphanius fasciatus* (Valenciennes, 1821): UFRJ 4019, 3; Italy: Salina di Ravenia. *Aphanius splendens* (Kosswig & Sözer, 1945): CAS 168742, 4, 26.3-33.2 mm SL; Turkey: Toparta Province, Golcuk. Tribe Cyprinodontini: *Cualac tesselatus* Miller, 1956: CAS(SU) 50213, 1; Mexico: San Luis Potosi, La Media Luna, near Río Verde. *Cyprinodon macrolepis* Miller, 1976: CAS 168750, 1; Mexico: Chihuahua, Jiménez. *Floridichthys polyommus* Hubbs, 1936: UFRJ 3425, 4; Mexico: Yucatan, near Río Lagartos. *Garmanella pulchra* Hubbs, 1936: UFRJ 3426, 4; Mexico: Yucatan, lagoon near Río Lagartos. *Jordanella floridae* Goode & Bean, 1879: UFRJ 3904, 1; USA: Florida. *Megupsilon aporus* Miller & Walters, 1972: UFRJ 3427, 4; Mexico: Nuevo Leon, El Potosi. Tribe Orestiini: *Orestias agassizii* Valenciennes, 1846: UFRJ 3048, 1; Bolivia: Copacabana, Lago Titicaca. *Orestias albus* Valenciennes, 1846: UFRJ 3894, 1; Peru, Cuzco. *Orestias crawfordi* Tchernavin, 1944: UFRJ 3046, 1; Bolivia: Copacabana, Lago Titicaca. *Orestias gilsoni* Tchernavin, 1944: UFRJ 3054, 5; Bolivia: Copacabana, Lago Titicaca. *Orestias ispi* Lauzanne, 1981: UFRJ 3044, 5; Bolivia: Copacabana, Lago Titicaca. *Orestias luteus* Valenciennes, 1846: UFRJ 3051, 2; Bolivia: Copacabana, Lago Titicaca. *Orestias mulleri* Valenciennes, 1846: Bolivia: Copacabana, Lago Titicaca.